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Rumination of different-sized particles in muskoxen (*Ovibos moschatus*) and moose (*Alces alces*) on grass and browse diets, and implications for rumination in different ruminant feeding types

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Running head: Rumination in muskoxen and moose

Abstract

The obligatory, periodic regurgitation of forestomach material and its subsequent re-mastication is the hallmark of the most diverse extant large herbivore group, the ruminants. Although the process of rumination is well understood in domestic species, differences between free-ranging wild ruminant species, for example of different body size or different feeding type, remain speculative to date. Here we investigate the proportion of plastic particles of varying size (1, 10 and 20 mm) and density (1.03, 1.20 and 1.44 mg/ml) that are recovered intact or ruminated-upon after insertion into the reticulorumen (RR) of domestic cattle (*Bos primigenius f. taurus*) on grass silage, and of muskoxen (*Ovibos moschatus*; n=4) and moose (*Alces alces*; n=2) both fed browse and grass diets. In the three species, the proportion of particles leaving the RR intact depended on particle size, with density showing no effect in this study. The major proportion of 1 mm particles was excreted intact, whereas intact 10-20 mm particles were only excreted sporadically, and not in all animals. Intact particles were mostly found in the initial samples after marker application, and mean retention times of intact particles were always shorter than those of ruminated particles. There were no differences between moose and muskoxen, but diet had a significant effect, with a higher proportion of 1 mm particles ruminated upon on the grass diet in both species, indicating a higher 'filter-bed effect' with entrapment of small particles in a fibre mat in the RR on a grass diet. Given that less particles were ruminated on the grass diet, one could either assume that free-ranging browsers ruminate less than grazers on similar food intakes (or that they have higher food intakes at similar levels of rumination). The existing data on time-budgets of free-ranging ruminants, however, does not suffice to test these hypotheses. The fact that indication of a 'filter-bed effect' was also detectable in moose raises the question whether adaptations described in 'cattle-type' ruminants really serve to re-inforce the processes of RR contents stratification and the 'filter-bed', or whether they are not rather directed at other aims, such as

maximizing microbial yield from the RR.

Key words: Rumen; Stratification; Digesta retention; Grazer; Browser; Activity budget

Introduction

According to their ecological and taxonomical diversity, Ruminatia are the most successful extant group of large mammalian herbivores (Heywood 2010). Their digestive physiology is characterised by the process of rumination, during which a certain fraction of digesta is regurgitated from the forestomach and chewed again in the oral cavity (Gordon 1968). In contrast to some other mammalian herbivores like macropods, koalas (*Phascolarctos cinereus*), capybaras (*Hydrochaeris hydrochaeris*), hyraxes or proboscis monkeys (*Nasalis larvatus*), in which facultative regurgitation and re-mastication of stomach contents has been reported sporadically and irregularly (and awaits further systematic investigation) (Moir et al. 1956; Mollison 1960; Barker et al. 1963; Hendrichs 1965; Lord 1994; Logan 2001; Logan 2003; Logan and Sanson 2003; Matsuda et al. 2011), this rumination is a mandatory and important part of the digestion process in functional ruminants - the Tylopoda (camels) and the Ruminantia (taxonomic ruminants) (Gordon 1968; Murphy et al. 1983).

It is generally assumed that the main purpose of rumination is to reduce the particle size of coarse material in order to facilitate its passage from the rumen. Rumination follows a circadian rhythm during which cattle spend about 8-9 hours a day ruminating (Welch 1982). This occurs more at night than during the day (Semiadi et al. 1994), but also to some extent during the day, in particular during the afternoon resting period (Gordon and McAllister 1970; Woodford and Murphy 1988). Rumination is not only an obligatory process in any ruminant's digestion; it is also considered a behavioural need in cattle irrespective of their rumen load. If deprived of the possibility to manipulate their feed orally (by eating and

67 ruminating), individuals can develop stereotypies (Lindström and Redbo 2000) and a lack of
68 rumination-eliciting fibre leads to a behaviour called sham-rumination (Campion and Leek
69 1997).

70 Their chewing efficiency enables ruminants to achieve extremely small digesta particle sizes
71 and corresponding high digestive coefficients at relatively high food intakes (Clauss et al. 2009d;
72 Schwarm et al. 2009b). Ruminants actually achieve, for their body size, the smallest faecal
73 particles among mammalian herbivores (Fritz et al. 2009). The proportion of time spent
74 ruminating depends on the type of food (Welch and Smith 1969b; Welch and Smith 1970), with
75 more rumination occurring on higher-fibre forages (Murphy et al. 1983; Renecker and Hudson
76 1989; Wenninger and Shipley 2000). As rumination time increases on forages of higher fibre
77 content, intake decreases (Welch 1982; Renecker and Hudson 1989). This has been considered
78 the underlying reason for an intake constraint in ruminants; however, it should be remembered
79 that forage intake decreases with decreasing forage quality also in non-ruminant herbivores
80 (Meyer et al. 2010).

81 The rumen of domestic ruminants is usually stratified in different layers, with a fibre mat
82 below a gas dome and above a fluid layer (Baumont and Deswysen 1991; reviewed in
83 Hummel et al. 2009). This stratified structure is due to buoyancy characteristics of ingested
84 forage particles (i.e. their propensity to float or sediment) (Sutherland 1988) and represents a
85 dynamic state submitted to formation processes that will vary depending on the type of forage
86 ingested and on time after feeding (Hummel et al. 2009). However, a stratification of rumen
87 contents is not found among all wild ruminants. Hofmann (1973) stated that the reticulo-
88 rumen (RR) contents of grazing wild ruminants are stratified whereas those of browsing wild
89 ruminants are not. Several later investigations supported this concept (Renecker and Hudson
90 1990; Tschuor and Clauss 2008; Clauss et al. 2009a; 2009b; 2009c) and suggest that the RR
91 contents of browsing ruminants stratify to a much lesser degree than that of grazers. With

92 respect to this difference in rumen physiology, Clauss et al. (2010c) suggested to classify
93 ruminants into ‘cattle-type’ (with stratified RR contents) and ‘moose-type’ (without stratified
94 RR contents) according to their forestomach physiology.
95 This raises the question whether the difference in RR physiology is also linked to
96 differences in the process of rumination. In particular, the findings of Nygren et al. (2001) and
97 Clauss et al. (2002) on differences in the faecal particle size of grazing and browsing
98 ruminants could suggest that, in animals without or with less stratified rumen contents,
99 rumination may not occur to the same extent as in animals whose rumen contents are actually
100 stratified. It has been shown since that differences between grazers and browsers in this
101 respect are probably an effect of diets fed in captivity (Hummel et al. 2008; Lechner et al.
102 2010) and that the sorting mechanism of particles in the reticulorumen itself also operates
103 without an evident rumen contents stratification (Lechner et al. 2010). Nevertheless, subtle
104 differences in the retention of certain particle fractions that indicate a more pronounced filter-
105 bed effect in grass-fed ruminants (Clauss et al. 2011) suggest that natural diets may have an
106 influence on the degree that digesta particles are submitted to rumination. Because rumination
107 is linked to the fibre content of the diet (Murphy et al. 1983), and because it has been often
108 assumed that browsers consume diets lower in fibre (Hofmann 1989; but see Clauss and
109 Dierenfeld 2008), it was suggested that browsers might spend less time ruminating than
110 grazers (Van Soest 1994, p. 54). A comprehensive comparative analysis is, however, lacking.
111 In this study, we aimed to test for differences in the proportion of particles (specifically
112 longer particles) leaving the RR intact or ruminated-upon in different ruminants, using plastic
113 markers. For this purpose, we used moose (*Alces alces*), which have been repeatedly
114 described as strict browsers (Schwartz 1992) and whose RR contents are not stratified
115 (Nygren and Hofmann 1990; Renecker and Hudson 1990; Tschuor and Clauss 2008; Clauss et
116 al. 2009b; 2009c; Lechner et al. 2010), and muskoxen (*Ovibos moschatus*), which

predominantly forage on grasses and sedges (Klein and Bay 1990; Larter and Nagy 1997), but also ingest high proportions of browse during summer (Staaland and Olesen 1992). Muskoxen resemble the 'cattle-type' ruminants morphologically (Staaland and Thing 1991; Staaland et al. 1997; Hofmann 2000; Mathiesen et al. 2000; Knott et al. 2004; Knott et al. 2005; Clauss et al. 2006) and physiologically (Adamczewski et al. 1993; Adamczewski et al. 1994a; Adamczewski et al. 1994b; Peltier et al. 2003; Barboza et al. 2006); their RR contents are stratified (Lechner et al. 2010), although probably not to the same extent as in cattle (Clauss et al. 2010a). The marker system was evaluated in advance in domestic cattle (*Bos primigenius* f. *taurus*), in which the stratified nature of RR contents structure has been well established (Hummel et al. 2009).

Materials and methods

This investigation was performed to expand the results previously presented on the excretion of plastic particles in different ruminants species by Clauss et al. (2011). Detailed information on the experimental procedures, particle preparation and sample treatment is given in Lechner et al. (2010) and Clauss et al. (2011).

Plastic particles

The evaluated plastic particles of different densities (1.03, 1.22 and 1.44 g/ml), sizes (1, 10 and 20 mm) and a common diameter of 0.7 mm consisted of polyethylene and barium sulphate. Nine different colours (yellow, orange, red, white, beige, black, violet, blue and green) were used for the purpose of differentiation of density/size combinations in the faeces. Because white and yellow particles could not be told apart after gut passage, both particle types could not be evaluated in cattle (i.e., we could not differentiate yellow particles of 1 mm and 1·03 g/cm^3 from white particles of 1 mm and 1·20 g/cm^3); in wild ruminants, only the

142 yellow but not the white particles were used (1·20 g/cm^3 particles were thus only represented
143 by 1 mm – black - and 20 mm – beige - particles). Additionally, black particles had been
144 particularly difficult to evaluate in cattle (see Clauss et al. 2011 for details).
145
146 *Animals, diets and experimental procedure*
147 Four adult, fistulated domestic oxen (mean ± SD 1238 ± 39 kg) of the Institute of Animal
148 Science of the University of Bonn, Germany, four fistulated, castrated male muskoxen (276 ±
149 23 kg) of the Robert G. White Large Animal Research Station, Institute of Arctic Biology,
150 University of Alaska, Fairbanks, AK, USA and two adult, fistulated female moose (345 ±13
151 kg) of the Alaska Department of Fish and Game at the Palmer Research Center, AK, USA
152 were used. The animals had been provided with ad libitum access to water, shade and their
153 respective feed. During the trial, the oxen were placed on a diet of grass silage, the muskoxen
154 were on a diet of either fresh mixed browse or grass hay in a crossover design, and the moose
155 were on an initial diet of fresh mixed browse, followed by a diet of grass silage a few months
156 later. Feeding was ad libitum. After an adaptation period to new diets, which lasted at least
157 14d, the plastic markers were applied as a pulse dose previous to the morning feed between
158 08:00 and 10:00 hours via the rumen cannulas. Subsequently, sampling of faeces was carried
159 out at progressively increasing intervals up to 240 h after marker dosage in oxen, 264-288 h in
160 muskoxen and 264-278 h in moose.
161
162 *Analysis*
163 Representative subsamples of faeces were dried, ground in a regular coffee grinder, which
164 does not affect the plastic particles (Kaske et al. 1992; Clauss et al. 2011), weighed, washed
165 over a sieve with a pore size of 0.5 mm and dried again before being sorted out by hand. After
166 the sorting, the plastic particles of each colour were weighed, and the mean retention times

(MRT) calculated (results presented in Clauss et al. 2011). The plastic particles were stored sorted according to the individual faecal samples they originated from.

For the current investigation, we examined the sorted particles a second time, in order to differentiate those that had stayed intact from those which had been ruminated. The distinction was made visually, based on the general shape of the particles: squeezed, extremely bended, and broken, as well as particles with obvious tooth marks, or particles that had been reduced in size, were considered as ruminated, while the particles that had retained their original size and shape were categorized as intact. The sorting was performed consistently by the same investigator (ML) under bright light conditions, with the help of a magnifying glass. Plastic particles of each colour and rumination status were weighed, and the concentration of markers was expressed as g particles/g faecal dry matter for each density and initial particle size. MRT for the toal digestive tract for each particle type was calculated as described in Clauss et al. (2011). Note that MRTs may be underestimates, because some markers were not completely excreted by the end of the collection period (an example is given in Fig. 1a), MRTs may be underestimates (Kaske and von Engelhardt 1990; Clauss et al. 2011). Results were expressed, for each individual animal and trial, as the proportion (per unit mass) of particles excreted intact (%intact, i.e., non-ruminated) of all particles excreted, and the mean retention time (MRT) of the intact particles as the proportion of the MRT of the ruminated ones [MRT_{intact}(%rum)].

Statistics

Data were analyzed using a hierarchically nested GLM (General Linear Models module, STATISTICA V8.0; (Statsoft_Inc 2007)). The categorical effect “Diet” was nested within the effect “Species”, with the continuous predictors “Particle density” and “Particle size” nested as third levels. “Individual” was included as a random effect (nested within Species) to

192 account for multiple treatments (diets) applied to each individual in the experiment, and
193 variation in "Intake" was controlled for by including this measure as a covariate. Residuals
194 from the analysis using the variables %intact and MRT_{intact}(%rum) as dependent variables did
195 not conform to normal distribution. Transformation (arcsine-, square root-, and log-
196 transformation) of the latter variables also yielded non-normal distribution of residuals, thus
197 the data were ranked for these analyses, recognizing that this non-parametric approach
198 reduces power of the statistical analysis. In all cases, residuals had equal variances across all
199 model terms (Levene's $P = 0.871$ to 0.999). Initial analyses revealed that the interaction term
200 of Particle density * Particle size had no significant effect on any of the 2 dependent variables
201 ($P = 0.406$ to 0.647); thus, this term was omitted from the final GLMs presented here. Effect
202 sizes are interpreted based on the partial eta-squared (η^2) of each nested term. *Post hoc*
203 evaluation of significant effects (nested terms) in the GLMs were evaluated using the
204 Bonferroni *post hoc* test (for the nested terms Individual[Species] and Diet[Species]), or
205 parameters (b) derived for each species and diet (for the terms Particle density[Diet[Species]]
206 and Particle size[Diet[Species]]) to evaluate whether slopes were positive, negative, or
207 horizontal (if their 95% confidence limits included zero).
208
209 *Literature survey*
210 In addition to the experimental data, we collected data from the literature on the time spent
211 ruminating in free-ranging wild ruminants. The literature search was performed using Google
212 Scholar and Pubmed, using ruminant genus names in combination with the terms
213 "rumination" and "activity budget" as search terms. Sources that did not observe rumination
214 directly, but only equated rumination time with resting time (Jarman and Jarman 1973;
215 Hanley 1982; Winterbach and Bothma 1998), were discarded, because detailed observations
216 have documented that time spent resting and ruminating are not the same (e.g. Belovsky and

217 Slade 1986; Renecker and Hudson 1989; du Toit and Yetman 2005). We used two data
218 collections on rumination in different-sized ruminants (Belovsky and Slade 1986; du Toit and
219 Yetman 2005), and supplemented these with data for additional species from individual
220 articles (Spinage 1968; Hendrichs and Hendrichs 1971; Grimsdell and Field 1976; Collins et
221 al. 1978; David 1978; Leuthold and Leuthold 1978; Pellew 1984; Renecker and Hudson
222 1989; Ginnett and Demment 1997; Taylor et al. 2006; Vymyslická et al. 2010), excluding
223 studies that noted a problem with representativeness of their data themselves (Oakes et al.
224 1992). Data referring to captive animals or animals kept in reserves with supplemental
225 feeding (e.g. Fakhar-i-Abbas et al. 2011) were not used. These data were combined with
226 estimates of the body mass and the percentage of grass in the natural diet of the species
227 (Clauss et al. 2010b; Müller et al. 2011a), and an effect of both of these parameters was tested
228 using correlation analysis and a GLM. Because no significant influence of either parameter
229 was evident, we did not apply further statistics accounting for phylogeny.
230
231 **Results**
232 Intact particles were mostly found in the initial samples after marker application (examples
233 documented in Fig. 1). Correspondingly, calculated mean retention times (MRT) for intact
234 particles were always shorter than those for ruminated particles in all three species (Table 1).
235 Whereas the major proportion of the smallest particles was excreted intact (see below), the
236 proportion of 10-20 mm particles excreted intact was only sporadic, with several animals
237 excreting no large intact particles at all (Table 1).
238
239 *Cattle*
240 The smallest and heaviest particles clearly constituted the highest percentage of intact
241 particles (%intact); actually, about 90% of the 1 mm, 1.44 g/ml particles were excreted intact.

242 In contrast, no distinction could be made between %intact of medium and large particles of
243 low (1.03 g/ml) and high (1.44 g/ml) density. However, there was a striking high percentage
244 of intact 10 mm particles of the middle density-class (Fig. 2a).

245 For the smallest, heaviest particles, MRT_{intact}(%rum) was close to 100%, indicating a
246 rather simultaneous excretion of the few ruminated particles with the intact ones. In contrast,
247 MRT_{intact}(%rum) was about 50% or lower for larger particles, indicating that if such particles
248 escaped the reticulorumen intact, they did so much sooner than those particles of their kind
249 that are ruminated upon, similar to the findings documented in Fig. 1. This was particularly
250 pronounced for the lightest particles (Fig. 2b).

251

252 *Muskoxen and moose*

253 The most important factor influencing both %intact and MRT_{intact}(%rum) was particle size (P
254 < 0.0001; $\eta^2 = 0.81$ for %intact, 0.32 for MRT_{intact}(%rum); Table 2), entailing a decline in the
255 fraction of markers escaping intact with increasing particle size in both species on both diets
256 (Fig. 3), and also an increase in MRT_{intact}(%rum) with decreasing particle size (Fig. 4). The
257 low importance of all variables aside from particle size is emphasized by huge data overlaps
258 across species, diets, and particle densities. Although particle density also had a significant
259 effect on both measures ($P = 0.020$ and 0.027), this only occurred in the first measure because
260 of a negative slope for muskoxen fed grass (Fig. 3a), and in the second because of a positive
261 slope for moose fed grass (Fig. 3c). Slopes included zero at 95% confidence for all other
262 cases. However, these effects were probably non-linear, especially particle size which clearly
263 shows a decline in %intact over an increase from 1 to 10 mm, but much less change across
264 larger particle sizes (Fig. 3). This non-linearity might also account for the inconsistent results
265 across species and diets.

Most other effects were either not significant in these analyses, e.g. food intake (P = 0.433 and 0.791), or only approached significance perhaps due to low power of the non-parametric analyses, e.g. diet (P = 0.707 and 0.111). However, in the case of the diet effect, a higher % of intact markers (less efficient rumination) for both species fed browse than when they were fed grass is visually apparent for the smallest particle size (Fig. 3). Restricting our analysis to include data only for the smallest particle size revealed a significant and strong effect of diet on %intact ($P < 0.001$; $\eta^2 = 0.48$).

Finally, our analyses found no evidence for a difference in %intact between the two species (P = 0.484), although MRT_{intact}(%rum) was significantly higher in moose than in muskox ($P < 0.001$), and showed there were no differences in either proxy for rumination efficiency among individuals of either species (Table 2; note that P = 0.037 for the "Individual" term for %intact, but *post hoc* tests revealed no significant differences between individuals *within* either species; P = 0.359 to 0.999).

Literature data

In the literature, even a very small ruminant as the dikdik (*Madoqua kirki*) is reported to ruminate for 6 hours per day or 25% of its activity budget (Hendrichs and Hendrichs 1971). Similarly, another small ruminant, the blue duiker (*Cephalus monticola*), was observed to ruminate 5.6 hours per day or 23% of its activity budget in captivity on a browse-only diet (Wenninger and Shipley 2000; not included in the evaluation of free-ranging specimens). In general, there is large variation in observation methods, which might preclude meaningful analyses of data collated from various sources (du Toit and Yetman 2005). In particular, many observers could not determine nightly activity budgets, but existing data suggests that night-time rumination may not only constitute a higher proportion of the activity budget than during daylight (Collins and Smith 1989), but that this difference also changes with seasons (Ginnett

and Demment 1997). Seasonal variation in rumination was evident in basically any study that included different seasons, with a lower proportion of rumination occurring during the vegetative season; Renecker and Hudson (1989) could link this to the cell wall content of the diet.

There was no correlation between body mass (BM) and the proportion of time spent ruminating for wet season data ($R = 0.20$, $P = 0.392$), data averaged for all seasons ($R = 0.34$, $P = 0.140$), or the overall minimum ($R = -0.02$, $P = 0.942$; Fig. 5a). The percentage of grass in the natural diet (%grass) was also not correlated to the proportion of time spent ruminating for wet season data ($R = 0.31$, $P = 0.182$) or data for all seasons ($R = 0.14$, $P = 0.553$), but there was a significant correlation with the overall minimum ($R = 0.46$, $P = 0.041$; Fig. 5b). In the GLM with the overall minimum proportion of observed time spent ruminating as the dependent variable and BM and %grass as covariables, BM again was not significant ($F_{2,17} = 0.217$, $P = 0.647$) but %grass was ($F_{2,17} = 4.864$, $P = 0.041$). When comparing data on the measured or reconstructed neutral detergent fibre (NDF) content of forage diets fed in captivity or observed in the wild, as linked to the observed time spent ruminating, no difference between animals of different feeding types is evident (Fig. 6). Whereas there seems to be a clear increase in rumination time with forage fibre content for NDF levels of up to 50 % in dry matter, the pattern became less evident above that fibre level. The general impression is that rumination levels off at 8 hours per day and rarely exceeds 10 hours.

Discussion

Rumen physiology

The present study demonstrates no significant distinction between the species regarding the proportion of ruminated particles, regardless of their evident difference in digesta retention times (Lechner et al. 2010; Clauss et al. 2011; cf. Fig. 1). These results corroborate the

316 interpretation of Lechner et al. (2010) (from the same trials, but using a different marker
317 system) who also reported no obvious difference in the efficiency of the sorting mechanism
318 and rumination between the 'cattle-type' and the 'moose-type' species. The ruminant
319 digestive physiology is generally marked by a particle size reduction of the digesta in the
320 reticulorumen (RR) via rumination.

321 In the ruminant literature, the term "critical size threshold" has been used to describe the
322 particle size above which particles are very unlikely to leave the RR. This threshold was
323 reported to be about 1.18 mm in sheep (Poppi et al. 1980), 3.6 mm in cattle (Shaver et al.
324 1988) and about 0.3 mm in dik-diks (Hebel et al. 2011), suggesting an increase in particle size
325 escaping from the RR with body mass that is also noticeable in faecal particle size of captive
326 wild ruminants (Fritz et al. 2009). The fact that the majority of very small particles were
327 excreted intact in this study supports the validity of a threshold. Whereas retention of particles
328 between 1 and 10 mm appears to follow a size-gradient (reviewed in Clauss et al. 2011), it is
329 generally assumed that above a large particle size threshold of about 10 mm, particle size has
330 no further systematic influence on the selective retention and rumination of large particles
331 (Kaske et al. 1992; Schwarm et al. 2009a; Clauss et al. 2011). Our findings show, however,
332 that the difference between 10 and 20 mm leads to a very small but detectable difference in
333 the proportion of particles that leave the RR intact (Fig. 2, 3). In contrast to findings by
334 desBordes and Welch (1984), density had no evident effect on whether particles were
335 ruminated or passed intact. These authors had reported a lower proportion of intact particles
336 in the lighter markers, which is plausible due to these particles' updrift and hence tendency to
337 locate themselves in the fibre mat and be regurgitated. In our study, this effect was evident in
338 the smallest particles, but not significant, similar to observations by Kaske et al. (1992) who
339 also found no significant effect of density in their sheep. Due to a similar trial with plastic

markers in cattle, Stetter Neel et al. (1995) concluded that other factors than density determined the passage of particles from the RR.

Those particles that leave the RR intact usually do so earlier than ruminated ones of the same particle class. Because this effect is particularly evident for the larger-sized particles, the resulting interpretation is that if the odd large particle does escape rumination, it does so at the very beginning of the digestive process. This was also evident in other studies using plastic markers (desBordes and Welch 1984; Kaske et al. 1992). The most likely explanation for this phenomenon is that the high RR fill, as experienced during and immediately after food intake, can create conditions where the sorting mechanism is less effective. RR outflow is highest during the intake of new food (Balch 1958), and a higher food intake level is generally associated with the escape of larger particles from the RR (Shaver et al. 1988). This also matches seasonal changes in faecal particles in free-ranging moose, in which a higher proportion of larger particles occurs during the season of high food intake (Nygren and Hofmann 1990; Nygren et al. 2001). As markers were applied in this study directly prior to the morning feeding, we speculate that during the first meal some of the larger particles were dislocated within the RR so that they had a chance to escape; after equilibration of RR contents, the sorting mechanism generally prevented any further escape of large particles. These results thus suggest that the sorting mechanism in itself needs to be conceptualized as a dynamic process (Hummel et al. 2009).

The measurement of MRT_{intact}(%rum) was lower in moose than in muskoxen. This finding can be explained by the generally longer MRTs in muskoxen as compared to moose, irrespective of diet (Lechner et al. 2010; Clauss et al. 2011). A major factor for these longer MRTs is probably the volume of the RR. A 400 kg moose has a wet RR content mass of 39 kg (Clauss et al. 2003); in contrast, Barboza et al. (2006) report a wet RR content mass of 40 kg for a 292 kg muskoxen. It has been suggested that the generally stronger effect of particle

size on retention time in muskoxen than moose was an indication for an additional effect of RR contents stratification in the former species (Clauss et al. 2011). In that evaluation, the effect of the grass diet on the increased retention of low-density particles was additionally interpreted as an indication for the 'filter-bed effect' (Faichney 2006), in which particles apt for RR escape are additionally retained due to entanglement in the fibre mat. In the present evaluation, the effect of grass leading to a lower proportion of intact small particles was evident, indicating that in grass RR contents, small particles were more likely to be trapped and regurgitated than in browse RR contents, irrespective of the ruminant species. Because due to its fermentation characteristics, it pays to retain grass material longer than browse (Hummel et al. 2006), the physical effects of grass forage that lead to the mat formation and the 'filter-bed effect' thus themselves enhance an optimal utilization of grass particles, via the prolonged delay in the RR and further size reduction via rumination.

The 'filter-bed effect' was demonstrated experimentally in domestic ruminants, where the feeding of whole forages induced a more pronounced fibre mat and led to a prolonged retention of small, non-forage fibre particles in the RR (Grant 1997). Differences in the retention of small particles between different forages, similar to the difference between browse and grass in this study, have also been reported. McLeod et al. (1990) observed a quicker outflow of small particles when feeding a legume hay as compared to a slower outflow of small particles when feeding a grass hay – potentially due to the additional 'filter-bed effect' in grass RR contents. Kelly and Sinclair (1989) found that the boli of RR contents regurgitated for rumination contained a very low proportion of leaf particles when the sheep were fed legume diets, but proportions equal to that in the food when fed grass diets. Again, this indicates that smaller particles are retained longer in grass RR contents. These authors also demonstrated differences in particle shape between grass (longish particles) and legumes (more cuboidal particles) also observed between grass and browse (Clauss et al. 2011), and

390 linked these measurements to structural forage characteristics, in particular the orientation of
391 vascular bundles.
392 On the one hand, the fibre mat, RR contents stratification and 'filter-bed effect' will lead
393 to a more thorough digestion of grass forage. On the other hand, these factors will represent a
394 limitation that might prevent animals from maximizing food intake. Various
395 morphophysiological characteristics of 'cattle-type' ruminants have been suggested to
396 reinforce the tendency of grass forage to form a fibre mat and stratified RR contents (Clauss
397 et al. 2010c; Codron and Clauss 2010). However, the fact that certain indications of the 'filter-
398 bed effect', such as the longer retention of light particles on grass diets (Clauss et al. 2011), or
399 the lower proportion of particles escaping the RR intact on grass diets (this study) were
400 observed in both the 'moose-type' and the 'cattle-type' ruminant species could suggest that
401 such reinforcement of the 'filter-bed effect' is not existent. Alternatively, rather than
402 suspecting a reinforcement, the morphophysiological characteristics could also be conceived
403 as adaptations to compensate for disadvantageous side-effects of stratification and simply to
404 increase the efficiency of the RR system in the absence of secondary plant chemicals usually
405 associated with browse (Codron and Clauss 2010). In particular, the increased relative and, in
406 some 'cattle-type' species, even absolute fluid throughput through the RR could have positive
407 effects, such as a more intensive harvest of forestomach bacteria (Clauss et al. 2010c; Müller
408 et al. 2011b), but this adaptation might be limited to those animals not relying on exclusive
409 browse diets (Codron and Clauss 2010).
410
411 *Ruminant activity budgets*
412 Differences in rumination time have been documented between lactating and nonlactating
413 females (Blanchard 2005; Hamel and Côté 2008), and between males and females of various
414 species (Pellew 1984; Gross et al. 1995). Two studies that tested for a systematic effect of

415 species' body mass on the time spent ruminating failed to detect it (Belovsky and Slade 1986;
416 du Toit and Yetman 2005). Belovsky and Slade (1986) stated that the absence of such a
417 relationship *"is surprising since large ruminants are known to ruminate longer than small*
418 *ruminants relative to feeding time. This occurs because large herbivores tend to consume*
419 *foods of higher fibre content."* However, even if larger ruminants ingested diets of higher
420 fibre content (Codron et al. 2007), the range of fibre covered by natural diets of ruminants
421 may well be in the area where a strong relationship with rumination is not evident (Fig. 6).
422 Other factors, such as food intake level (e.g. Welch and Smith 1969a) – which may be subject
423 to seasonal variation -, might be more influential in this fibre range. Insecurity in the
424 measurement of rumination time due to difficulties in observing the behaviour at nighttime
425 (which accounts for the majority of all rumination activity), and variation in the relationship
426 of night vs. day rumination (Semiadi et al. 1994), which makes a calculation with a correction
427 factor impossible, potentially renders the measurement of rumination by observation so
428 inaccurate that the differences due to different dietary fibre levels might be overlooked.
429 A higher proportion of particles that pass through the RR un-ruminated on a browse diet
430 translates into two scenarios: either animals foraging on browse should spend less time
431 ruminating, or alternatively, if rumination times are similar, that these animals have a
432 generally higher food intake. Evidence for either scenario is scarce. Although the analysis of
433 minimum reported rumination times indicates the possibility that browsers do sometimes
434 ruminate less than grazers, the large overlap in the range of rumination times observed (Fig.
435 5), and the known insecurities associated with lack of measurements during night time in
436 many studies, make this interpretation less than convincing. A higher food intake in browsers
437 as compared to grazers has been suggested repeatedly (Baker and Hobbs 1987; Hummel et al.
438 2006), but not been proven to date.

439 The inclusion of browse leaves or legumes in a diet can lead to higher intakes in
440 muskoxen (Boyd et al. 1996), and intake on browse may be higher than that on grass forage
441 (Lechner et al. 2010). In impala, du Toit and Yetman (2005) found a higher ratio of feeding
442 time to rumination time during the season when the animals rely on browse as compared to
443 their grazing season. Similarly, the time spent feeding increased significantly in muskoxen
444 when adding browse to a grass pasture, whereas the time spent ruminating did not (Boyd et al.
445 1996).
446 To conclude, if connections between digestive physiology and behavioural activities in
447 different ruminant species are to be made, more detailed comparative datasets on feeding
448 related behaviours and food intake will be necessary.
449
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459
460
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Winterbach HEK, Bothma JdP (1998) Activity patterns of the Cape buffalo (*Syncerus caffer caffer*) at the Willem Pretorius Game Reserve, Free State. South African Journal of Wildlife Research 28:73-81

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751 Table 1. Median (range) mean retention time (in hours) of intact and ruminated plastic
752 particles of different specific density and length in cattle (n=4) on grass silage, and muskoxen
753 (*Ovibos moschatus*, n=4) and moose (*Alces alces*, n=2) fed either grass or browse diets.
754 Numbers in [brackets] indicate the number of animals that excreted particles of the
755 corresponding characteristics.

Particle density (g/ml)		---------- 1.03 ----------			---------- 1.20 ----------			---------- 1.44 ----------		
Particle length (mm)		1	10	20	1	10	20	1	10	20
Cattle	intact	-	55 (46,67)	70 (61,79) [2]	-	67 (60,93)	-	87 (79,103)	63 (56,88)	111 (43,138) [3]
	ruminated	-	152 (148,153)	158 (150,160)	-	125 (121,134)	-	102 (97,108)	116 (110,122)	137 (124,143)
Muskoxen										
Grass	intact	85 (62,98)	46 (30,64)	34 (30,76) [3]	45 (38,55)	-	73 (60,116) [3]	48 (39,55)	37 (34,51)	84 (59,108) [2]
	ruminated	150 (116,172)	152 (145,156)	164 (150,166)	82 (70,111)	-	134 (125,169)	86 (77,107)	124 (105,147)	118 (99,156)
Browse	intact	58 (51,61)	38 (31,55)	32 (26,47) [3]	39 (36,43)	-	39 (26,48)	39 (37,44)	38 (26,45)	48 (43,52) [2]
	ruminated	115 (97,134)	124 (104,175)	137 (108,191)	79 (70,82)	-	128 (91,173)	77 (73,93)	115 (93,145)	110 (88,158)
Moose										
Grass	intact	53 (42,54)	40 (34,46)	40 [1]	46 (44,48)	-	36 (33,38)	46 (46,46)	45 (36,53)	50 (38,62)
	ruminated	103 (99,107)	107 (106,108)	108 (108,108)	68 (64,71)	-	73 (69,76)	70 (67,73)	76 (69,82)	69 (63,74)
Browse	intact	31 (29,33)	22 (17,26)	43 (32,53)	32 (27,36)	-	22 (16,28)	27 (26,28)	22 (21,22)	30 (27,32)
	ruminated	78 (68,88)	76 (65,86)	77 (67,87)	47 (42,51)	-	57 (52,61)	48 (44,52)	60 (52,68)	57 (53,60)

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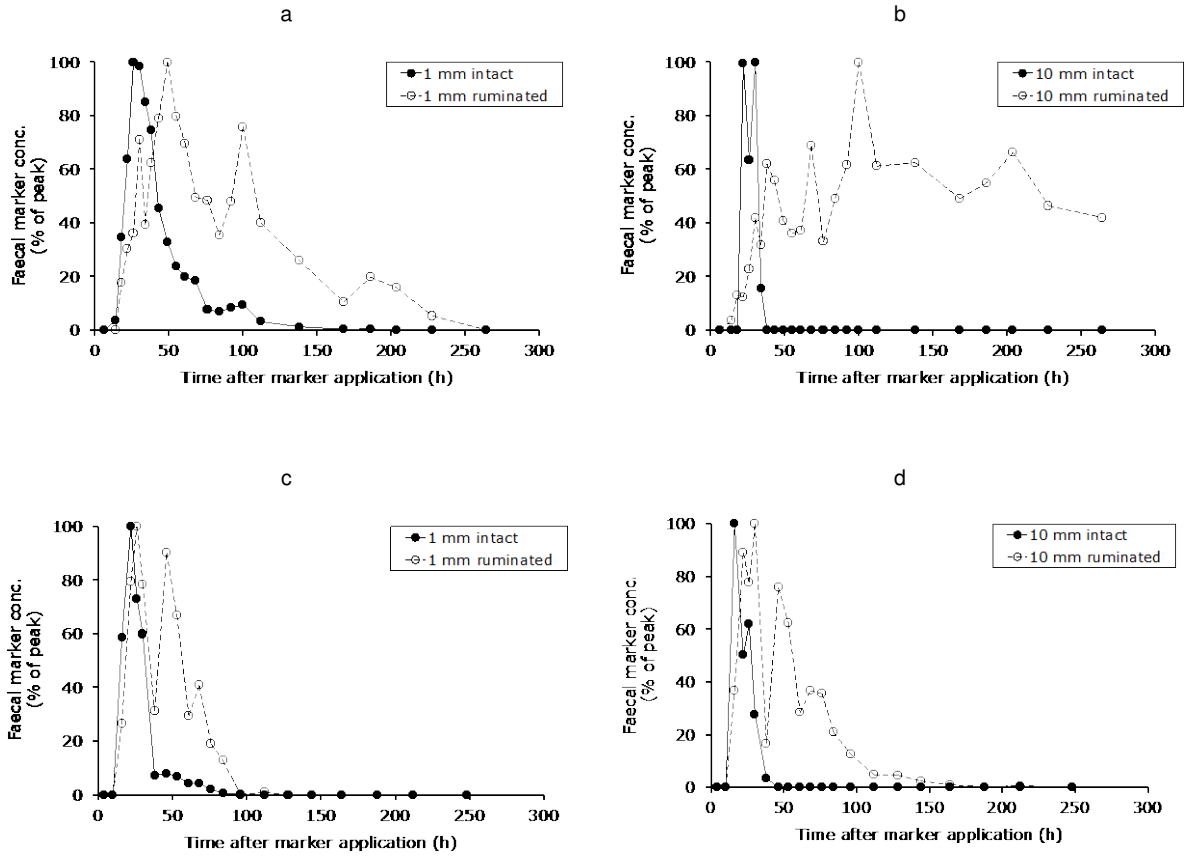
759

760 Table 2. Results of the final hierarchically nested general linear models for the percentage of
761 intact particles of all excreted particles (%intact, a measure of how much rumination occurred
762 for a particle type) and the mean retention time (MRT) of intact particles expressed as the
763 percentage of the MRT of ruminated particles (MRT_{intact}(%rum), a measure of how much
764 faster intact particles are excreted in relation to ruminated ones).

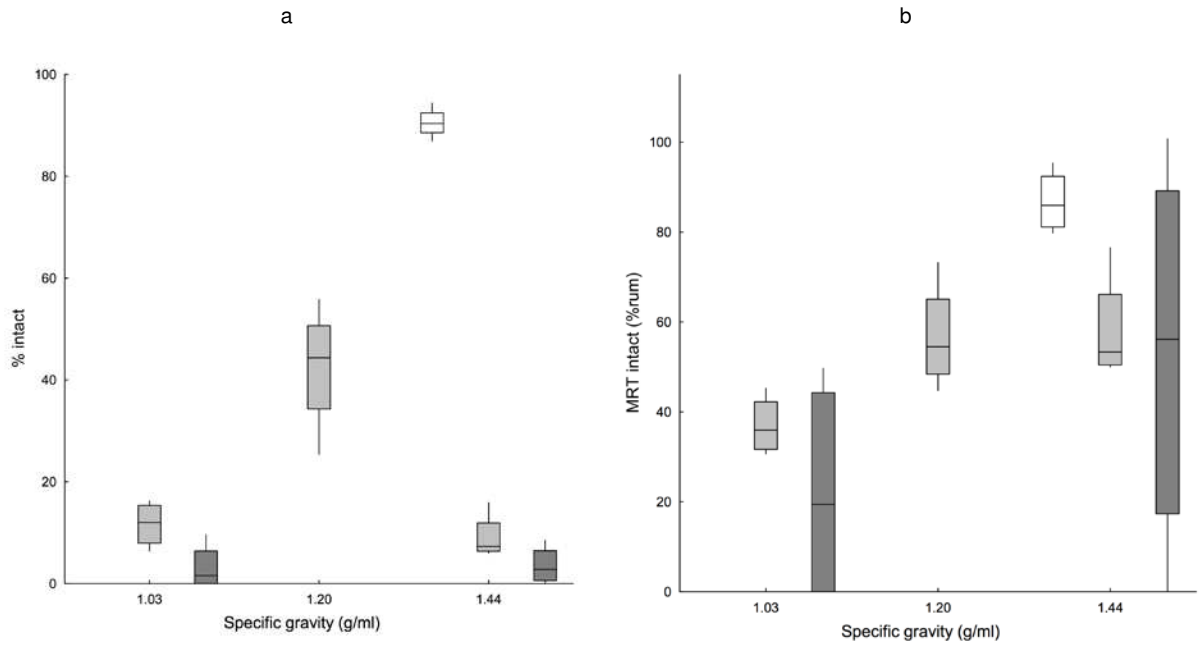
Effect	***df***	***F***	***P***	η^2	***post-hoc* or parameter slope (*b*)**
Rank %intact					
Species	1, 79	0.495	0.4838	0.01	n.a.
Individual(Species)	4, 79	2.698	0.0366	0.12	n.a.
Diet(Species)	2, 79	2.741	0.0707	0.06	n.a.
Particle density(Diet(Species))	4, 79	3.115	0.0196	0.14	-ve for muskox on grass *b* = 0 for other groups
Particle size(Diet(Species))	4, 79	83.980	<0.0001	0.81	-ve for both species on both diets
Intake	1, 79	0.622	0.4327	0.01	n.a.
Rank MRT_{intact}(%rum)					
Species	1, 79	13.302	<0.001	0.14	moose > muskox
Individual(Species)	4, 79	1.772	0.1428	0.08	n.a.
Diet(Species)	2, 79	2.264	0.1106	0.05	n.a.
Particle density(Diet(Species))	4, 79	2.902	0.0270	0.13	+ve for moose on grass *b* = 0 for all other groups
Particle size(Diet(Species))	4, 79	9.207	<0.0001	0.32	-ve for both species on both diets
Intake	1, 79	0.071	0.7908	0.00	n.a.

765 *Post hoc* comparisons using Bonferroni test (two-tailed a = 0.05); For the continuous effects (particle density and
766 particle size), parameters are considered significant if 95% CI excludes zero (*b* = 0 indicates zero included in the
767 95% CI); n.a. = no significant differences in the multiple comparisons tests, or effect not significant.
768



769

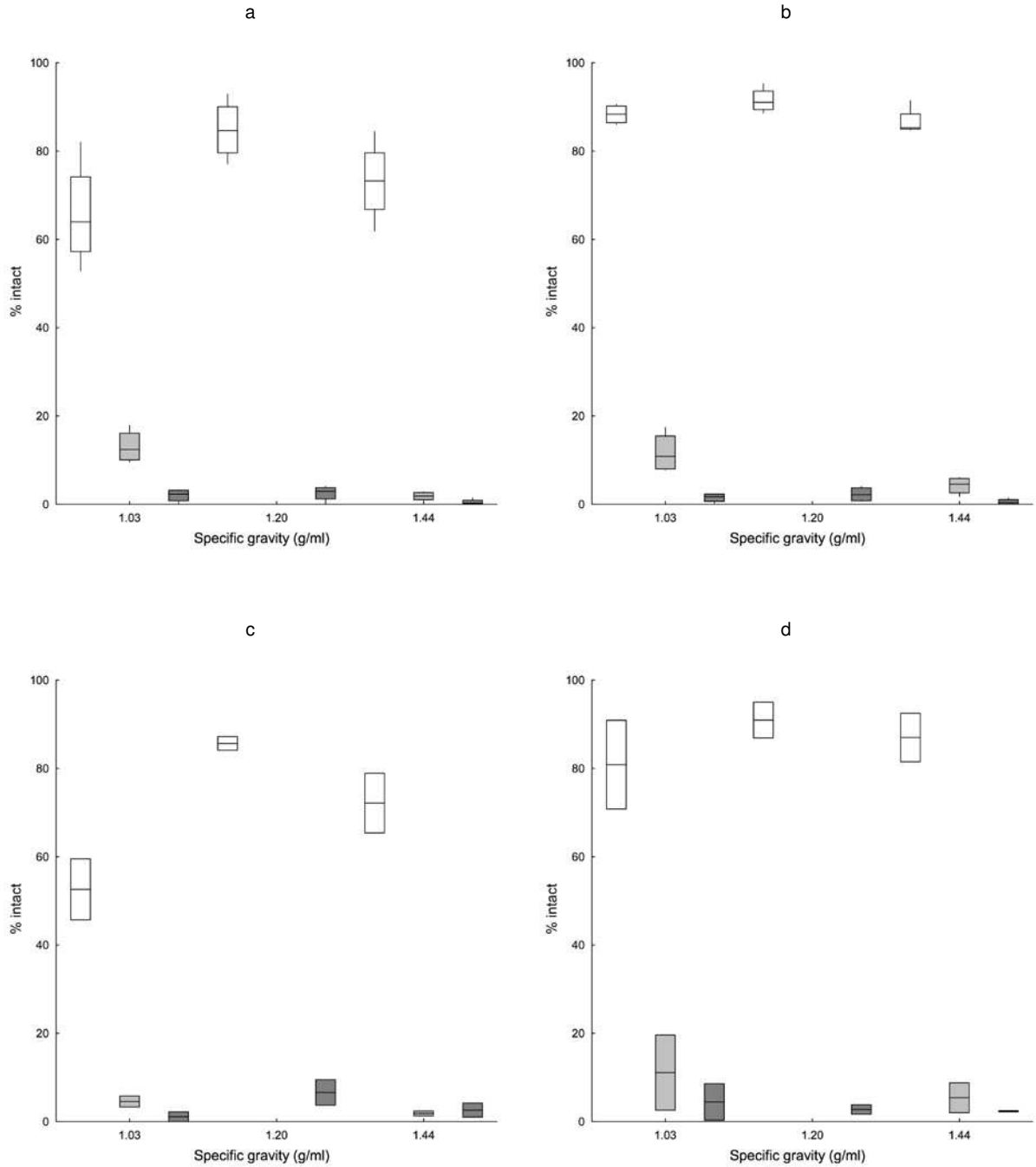
770 Figure 1. Examples of excretion curves for small (a,c) and large (b,d) plastic particle markers
771 with a specific gravity of 1.44 g/ml excreted either intact or ruminated upon in one of the
772 muskoxen (a,b) and the moose (c,d) of this study on browse diets. Note that intact particles
773 are excreted earlier than ruminated particles, and the generally quicker excretion in moose.



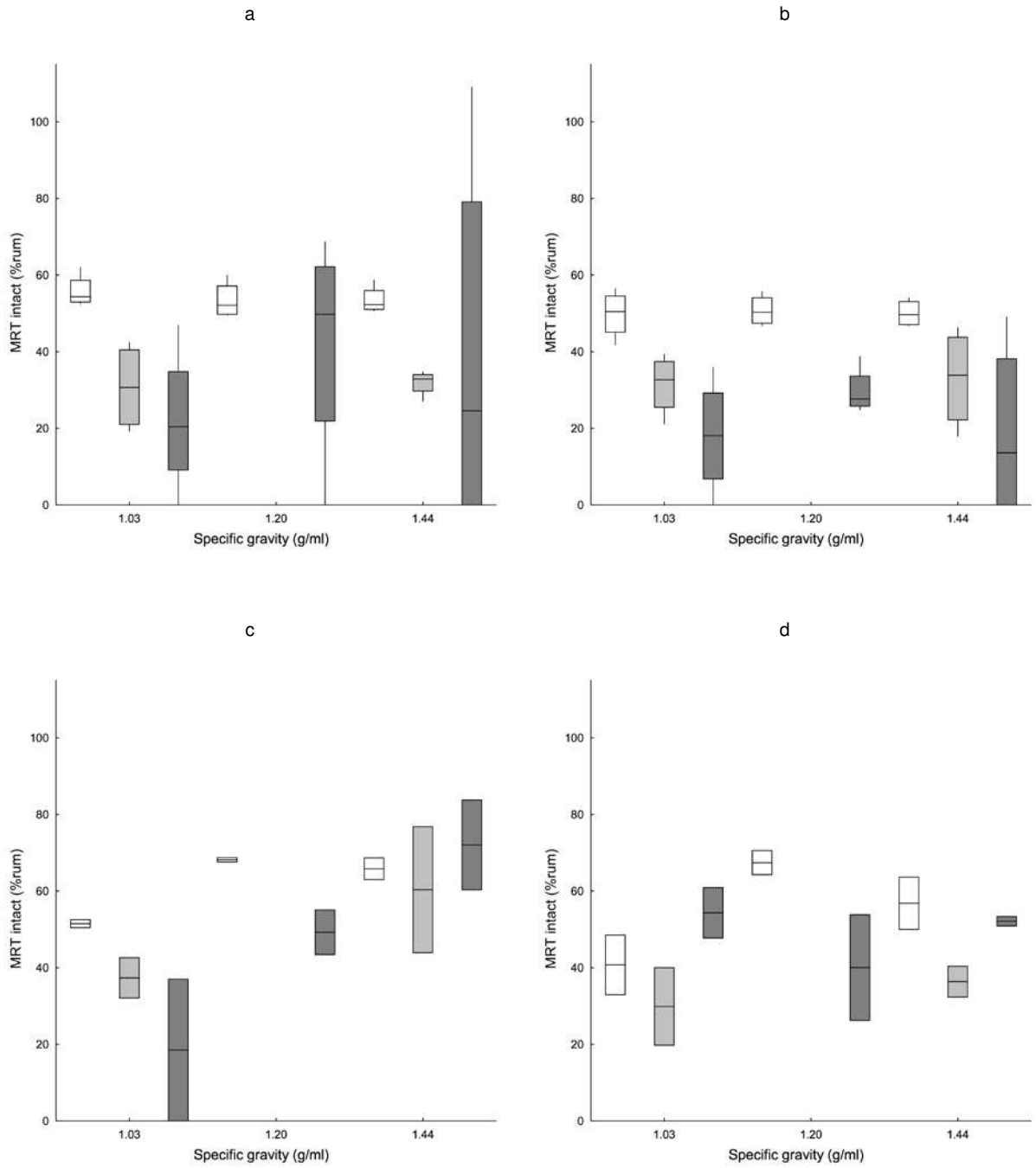
774

775 Figure 2. a) The percentage of intact particles (of all excreted particles; %intact), and b) the
776 mean retention time (MRT) of intact particles (as a percentage of the MRT of ruminated
777 particles; MRT intact (%rum)) in domestic cattle fed grass silage, for particles of varying
778 specific gravity and length (white = 1 mm, light grey = 10 mm, dark grey = 20 mm).
779 Horizontals are medians, boxes are interquartile ranges, whiskers are min-max ranges.

780



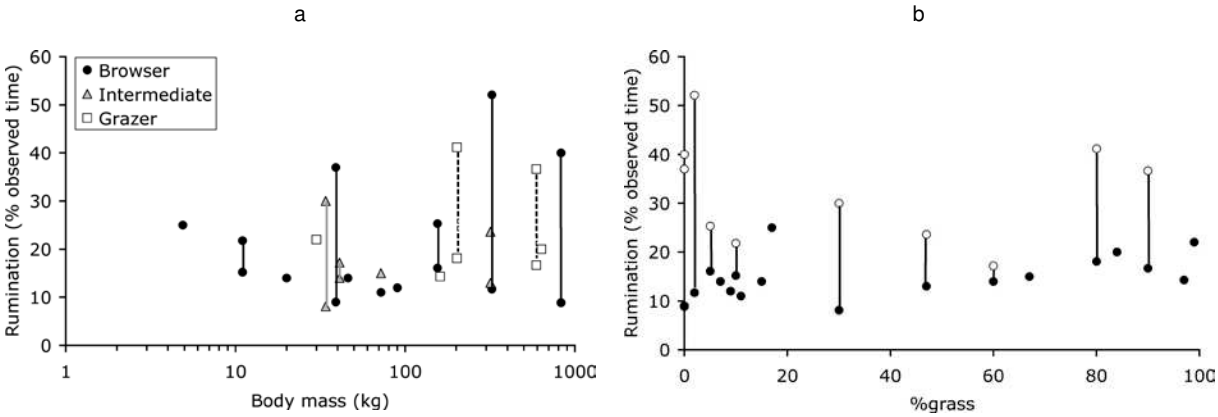
781 Figure 3. Percentage of intact (non-ruminated) particles in muskoxen (*Ovibos moschatus*) on
782 a) grass hay and b) on browse, and of moose (*Alces alces*) on c) grass silage and d) on
783 browse, for particles of varying specific gravity and length (white = 1 mm, light grey = 10
784 mm, dark grey = 20 mm). Horizontals are medians, boxes are interquartile ranges, whiskers
785 are min-max ranges.



786

787 Figure 4. Mean retention time (MRT) of intact particles (as a percentage of the MRT of
788 ruminated particles) in muskoxen (*Ovibos moschatus*) on a) grass hay and b) on browse, and
789 of moose (*Alces alces*) on c) grass silage and d) on browse, for particles of varying specific
790 gravity and length (white = 1 mm, light grey = 10 mm, dark grey = 20 mm). Horizontals are
791 medians, boxes are interquartile ranges, whiskers are min-max ranges.

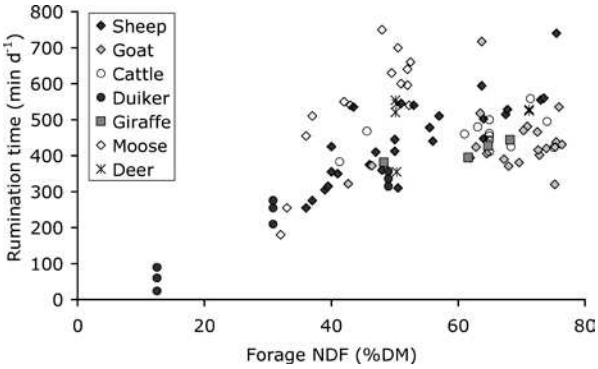
792



793

794 Figure 5. Relationship between a) body mass and b) the percentage of grass in the natural diet
795 and the proportion of rumination of observed time (given, when available, as the minimum
796 and maximum observation) for various free-ranging wild ruminant species. Intermediate
797 feeders are defined as species ingesting > 20% and <80% grass. *Bison bison*, *Cervus elaphus*,
798 *Ovis canadensis*, *Odocoileus hemionus*, *O. virginianus*, *Antilocapra americana* (all Belovsky
799 and Slade 1986), *Cervus canadensis* (Collins et al. 1978), *Antidorcas marsupialis* (David
800 1978), *Raphicerus campestris*, *Aepyceros melampus*, *Tragelaphus strepsiceros* (all du Toit
801 and Yetman 2005), *Syncerus caffer* (Grimsdell and Field 1976), *Litocranius walleri* (Leuthold
802 and Leuthold 1978), *Giraffa camelopardalis* (Leuthold and Leuthold 1978; Pellew 1984;
803 Ginnett and Demment 1997; du Toit and Yetman 2005), *Madoqua kirki* (Hendrichs and
804 Hendrichs 1971), *Alces alces* (Renecker and Hudson 1989), *Kobus ellypsiprymnus* (Spinage
805 1968), *Palea capreolus*, *Redunca fulvorufula* (Taylor et al. 2006), *Alcelaphus buselaphus*
806 (Vymyslická et al. 2010).

807



808

809 Figure 6. Relationship between forage neutral detergent fibre (NDF) concentration and the
810 daily time spent ruminating in different ruminant species. Domestic sheep (Murphy et al.
811 1983, read from graph; McSweeney and Kennedy 1992), domestic goat (McSweeney and
812 Kennedy 1992; Coleman et al. 2003), domestic cattle (Bae et al. 1981; Bae et al. 1983; Jaster
813 and Murphy 1983; Shaver et al. 1988; McLeod et al. 1990; Luginbuhl et al. 2000), *Alces alces*
814 (Renecker and Hudson 1989, read from graph), *Cephalus monticola* (Wenninger and Shipley
815 2000, read from graph), *Cervus elaphus* and *C. unicolor* (Semiadi et al. 1994; Howse et al.
816 1995), *Giraffa camelopardalis* (Pellew 1984).